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# COMMON INSHORE BARNACLE CYPRIDS OF THE OREGONIAN FAUNAL PROVINCE (CRUSTACEA: CIRRIPEDIA)[1]

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*Abstract.*—Seven species of barnacle cyprids from field collections are illustrated, described, and compared. Cyprids described in detail are *Pollicipes polymerus, Chthamalus dalli, Balanus glandula, Balanus nubilus*?, and *Semibalanus cariosus*. Previous descriptions of the cyprids of *Balanus crenatus* and *Balanus improvisus* are amplified. Ecological notes and a key to the species are also given.

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The sessile stages of barnacles, their systematics and biology, have received considerable study for more than a century. Yet our knowledge of barnacle larvae has advanced slowly, despite their prominence in inshore waters, and their importance in unifying the four orders of Cirripedia. This situation has prevailed for two main reasons. First, larvae have been regarded historically as mere developmental stages in the life history of the all-important adult. Fortunately, many biologists now view them as functional, independent animals having important ecological roles, and deserving of more detailed study.

Second, barnacle larvae, especially cyprids, have proved difficult to distinguish and to identify (Pyefinch, 1948; Costlow and Bookhout, 1958; Moyse, 1961; Crisp, 1962; Barker, 1976; Lang, 1979). Specimens collected from plankton samples are not easily linked to known adults, and laboratory-reared cyprids frequently differ from their "wild" counterparts in size and shape (Freiberger and Cologer, 1966; Lang, 1979). Workers dealing with only one or two species have usually lacked the comparative material necessary for good descriptions, and most studies on barnacle larvae have focused on the naupliar stages rather than on the cyprids. Thus, illustrations and measurements of cyprids are fairly common in the literature, but full descriptions are rare.

This paper describes seven species of cyprids from the Oregonian Province. These are *Pollicipes polymerus, Chthamalus dalli, Balanus glandula, Balanus crenatus, Balanus improvisus, Balanus nubilus*?, and *Semibalanus cariosus*. Although some of these species have been illustrated or briefly

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described previously, they are included here either because earlier accounts do not compare them to other Oregonian forms, or because this study has revealed characters not observed before. Also included here are notes on identification, distribution, and abundance, and a key to the species.

## Materials and Methods

Unless otherwise noted, cyprids were collected in Bodega Harbor, California, from April 1975 to November 1978. Bodega Harbor is a small, partially closed embayment located about 100 km north-northwest of San Francisco. It has coastal water conditions and considerable tidal exchange. The collection site was the U.S. Coast Guard wharf, near the mouth of the harbor. Of the cyprids examined from Bodega Harbor, 99.93% were referable to the species described here (excepting *Balanus improvisus* and *Semibalanus cariosus*); 0.07% were of uncertain identity.

Samples were taken with a gasoline-driven pump, fitted with an intake hose, and filtered through a 158 $\mu$m mesh plankton net. In 1976 and 1977, cyprids were collected at three depths: 30 cm above the bottom (depth 3–5 m, depending on tidal level), 15 cm below the surface, and midway between the surface and bottom. Volumes sampled at each depth were 1.0 $m^3$. Samples were collected halfway between the predicted times of lower low water and higher high water levels on flood tides. Sampling frequency was about every eight days. Cyprid densities are based on samples collected from October 1976 to November 1977. Adult distributions are modified from Newman (1979a).

Identification of cyprids was accomplished in several different ways. First, some identifications were based primarily on laboratory rearing: either cyprids were raised from embryos taken from identified adults, or field-collected cyprids were induced to settle and grow into identifiable juveniles. Second, spatial and temporal coincidences of large numbers of cyprids and newly settled juveniles were frequently observed in the field. The cyprids were later identified by following cohorts of juveniles through time until they became identifiable. Third, some cyprids could be identified by comparing them to illustrations or descriptions in the literature, or by comparing them to cyprids identified in other parts of the world. Finally, considerable information on the local and geographical distributions of adults was available. However, caution must be exercised in inferring cyprid identifications from large-scale distributions of adults. Identifications based on several different kinds of evidence are likely to be most reliable.

Cyprids were studied with dissecting and compound microscopes for descriptive characters. Special attention was directed towards taxonomic features not requiring high power microscopy and microdissection. These features were carapace shape, size, and sculpturing, together with special

pigmentation patterns. Shape and size characters were initially observed by carefully aligning the body in side and dorsal views. This alignment was accomplished by sticking the animal to a dish with a tiny dab of silicone grease, and then orienting it so that the body was as horizontal as possible in dorsal view, and so that the compound eyes were superimposed in side view. Size measurements were made with a dissecting microscope fitted with an ocular micrometer and were representative of all cyprids collected in 1977, unless otherwise indicated. The measurements taken were length—from anterior to posterior carapace margins, depth—greatest distance between dorsal and ventral carapace margins, and width (breadth)—greatest distance between one side and the other. Special pigmentation characters, as referred to here, are those that appear to differ from general ground color and from color that may be associated with specific organs. These characters were observed on freshly killed cyprids, as well as formalin-preserved ones, because pigmentation characters sometimes fade in preservatives. Observation of sculpturing characters required the high dry magnification of a compound microscope. The drawings were made with the aid of a camera lucida.

Voucher specimens of the species described here have been placed in the National Museum of Natural History (USNM 181245–181251).

Subclass Cirripedia
Order Thoracica
Suborder Lepadomorpha
Family Scalpellidae
Subfamily Pollicipinae Zevina, 1978
*Pollicipes polymerus* Sowerby, 1833 (=*Mitella polymerus*)
Fig. 1

*Distribution.*—Adults: lower midtidal and low intertidal zones of wave-swept shores; on rocks and hard-shelled animals. Cyprids: throughout water column, mean density 10 $m^{-3}$; mainly in fall and winter. British Columbia south to Cape San Lucas, Baja California.

*Identification.*—(1) Cyprids reared in the laboratory from embryos, using the methods of Lewis (1975). (2) Juveniles and adults present on floating pier adjacent to Bodega Harbor collection site. (3) Cyprid illustrations in Broch (1922) and Lewis (1975), although Lewis's drawing does not resemble *P. polymerus*. Naupliar stages described and figured in Lewis (1975).

*Diagnosis.*—Small, mean length 494 $\mu$m. Translucent when fresh. Relatively translucent when preserved, with light orange cement glands posteroventral to compound eyes. No special pigmentation. Carapace profile relatively high in side view; anterior end broadly rounded; posterior end narrowly rounded; anterodorsal margin broadly curved; posterodorsal mar-

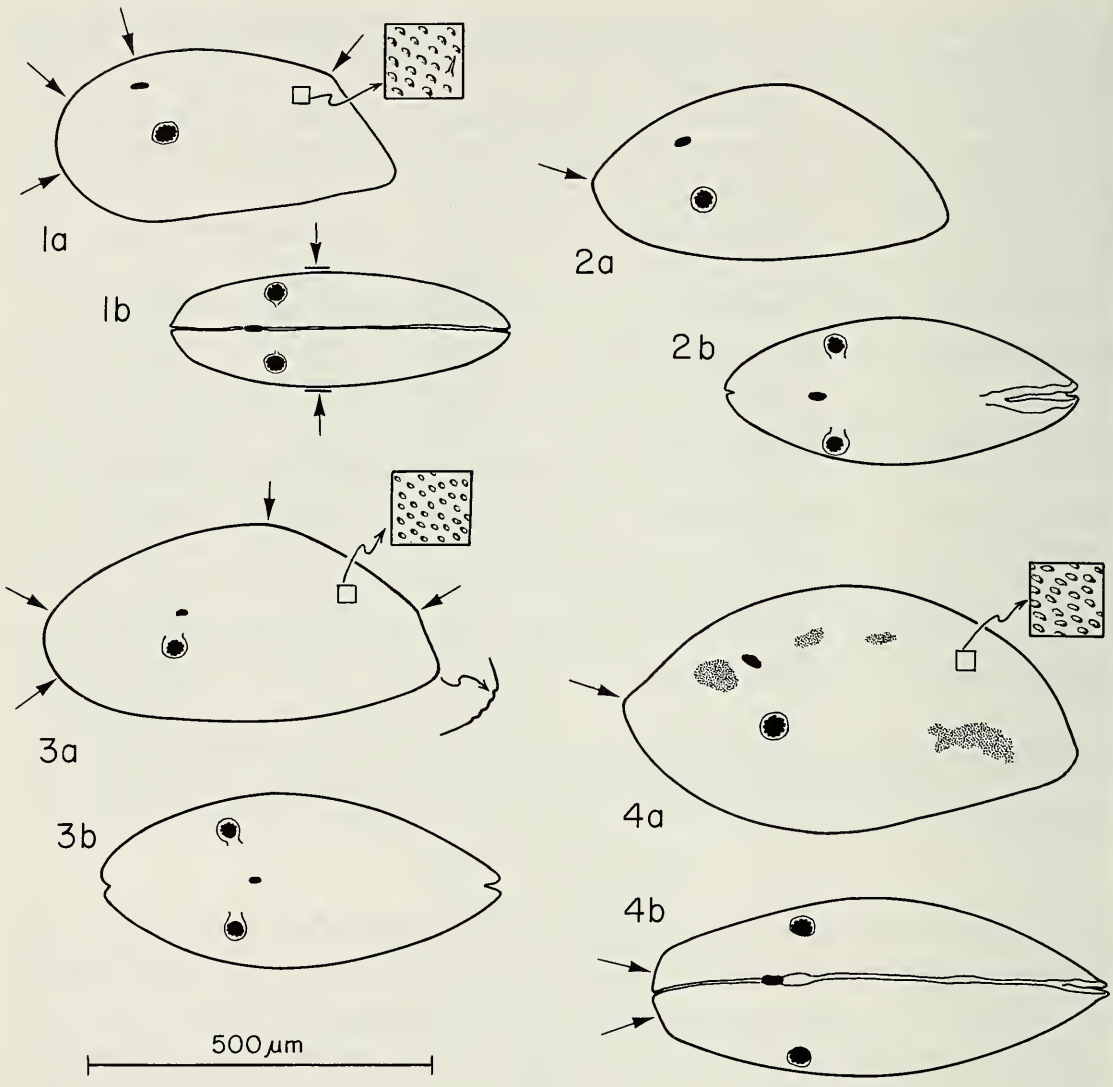
Table 1.—Sizes of barnacle cyprids in μm. Depth is the measurement between the dorsal and ventral carapace margins; width, the measurement between sides. Data are expressed as means; ranges are given in parentheses.

| Species | Collection site | Length | Depth | Width | n |
|---|---|---|---|---|---|
| *Pollicipes polymerus* | Bodega Harbor, California | 494 (420–520) | 256 (220–260) | 177 (160–200) | 50 |
| *Chthamalus dalli* | Bodega Harbor, California | 529 (440–580) | 270 (240–300) | 230 (200–260) | 50 |
| *Balanus glandula* | Bodega Harbor, California | 728 (640–780) | 388 (320–440) | 309 (240–360) | 50 |
| *Balanus crenatus* | Bodega Harbor, California | 852 (700–960) | 374 (300–440) | 328 (260–400) | 50 |
| *Balanus crenatus* | Point Barrow, Alaska | 1,001 (900–1,060) | 473 (400–520) | 450 (380–520) | 67 |
| *Balanus improvisus* | San Francisco Bay, California | 584 (540–610) | 304 (270–340) | 285 (250–320) | 25 |
| *Balanus nubilus*? | Bodega Harbor, California | 932 (800–1,000) | 431 (360–480) | 345 (280–400) | 50 |
| *Semibalanus cariosus* | San Juan Island, Washington | 1,111 (960–1,200) | 499 (420–560) | 493 (440–560) | 21 |

gin curved, breaking about two-thirds of the way towards posterior end; ventral margin broadly curved anterior to, and relatively straight posterior to, compound eyes. Carapace profile narrowly fusiform in dorsal view, mean width 177 μm; both ends broadly rounded. Entire carapace sculptured with uniform, rounded, regularly-spaced papillae (about 4.5 μm in diameter and 1.5 μm high) and occasional spine-like processes (about 7 μm high).

*Size variation.*—Mean length 494 μm, range 420 to 520 μm at Bodega Harbor, California (Table 1).

*Remarks.*—This cyprid is the smallest one discussed here, although its size overlaps broadly with that of *Chthamalus dalli.* It differs from the cyprids of *C. dalli, Balanus improvisus,* and most other species in having a broadly rounded anterior end in side view, a break in the posterodorsal margin, a narrow carapace profile in dorsal view, and a carapace sculptured with small papillae. The greatest depth of the carapace is at about the level of the compound eyes, rather than considerably behind this level as in the other species. The cyprid of *P. polymerus* is similar to the somewhat larger cyprid of *B. improvisus* in having a break in the posterodorsal margin, but differs in having the carapace sculptured with papillae rather than pits. The latter two species are also spatially separated, co-occurring mainly around the mouths of some enclosed bays.




Figs. 1–4. Lateral (a) and dorsal (b) views of barnacle cyprids. **1,** *Pollicipes polymerus;* **2,** *Chthamalus dalli;* **3,** *Balanus improvisus;* **4,** *Balanus glandula.* Insets show carapace sculpturing; pigmented areas are stippled. Straight arrows indicate some diagnostic characters used in the key.

Suborder Balanomorpha
Superfamily Chthamaloidea
Family Chthamalidae
Subfamily Chthamalinae
*Chthamalus dalli* Pilsbry, 1916
Fig. 2

*Distribution.*—Adults: intertidal zone of exposed and protected shores; on rocks, pier pilings, and hard-shelled animals. Cyprids: surface and mid-depths mainly, mean density 11 $m^{-3}$; mainly in summer and fall. Northern Japan and Alaska south to San Diego, California.

*Identification.*—(1) Juveniles reared in the laboratory from field-collected cyprids. (2) Adults present on pilings adjacent to collection site. Naupliar stages have not been described or figured.

*Diagnosis.*—Small, mean length 529 μm. Translucent when fresh, with paired, dark areas located about halfway between compound eyes and posterior end. Relatively translucent when preserved, but more opaque anteriorly; with prominent light brown cement glands posteroventral to compound eyes. No special pigmentation. Carapace profile relatively high in side view and peaked dorsally at midlength; anterior end narrowly rounded to angular; posterior end narrowly rounded; anterodorsal margin slightly curved; posterodorsal margin evenly curved; ventral margin curved anterior to, and slightly curved posterior to, the compound eyes. Carapace profile in dorsal view broadly fusiform, with both ends rounded. Carapace smooth, unsculptured.

*Size variation.*—Mean length 529 μm, range 440 to 580 μm at Bodega Harbor, California (Table 1).

*Remarks.*—This cyprid is most likely to be confused with those of *P. polymerus* and *B. improvisus,* which it overlaps in size. Unlike *P. polymerus,* the carapace profile peaks well behind the compound eyes in side view and is relatively wide in dorsal view. The carapace is glassy smooth, lacking the sculpturing of both *P. polymerus* and *B. improvisus* cyprids. In side view the cyprid of *C. dalli* also differs from that of *B. improvisus* in having a more angular anterior end and an evenly curved posterodorsal margin with no break. *C. dalli* is also probably similar to *Chthamalus fissus,* but the cyprid of the latter species is undescribed at present.

Superfamily Balanoidea
Family Balanidae
Subfamily Balaninae Newman, 1979b
*Balanus improvisus* Darwin, 1854
Fig. 3

*Distribution.*—Adults: low intertidal zone and subtidal areas in estuaries and some enclosed bays; particularly tolerant of brackish water; on rocks, pilings, and hard-shelled animals. Cyprids: mainly low in water column in estuaries and some enclosed bays (Bousfield, 1955; Mohammad, 1961); summer, also spring and fall (Weiss, 1948; Jones and Crisp, 1954; Blom, 1965; Sneli, 1972). Introduced into the North Pacific; Columbia River, Oregon south to the Salinas River, California; occasionally in harbors south of Point Conception; Ecuador, Japan, Australia, North and South Atlantic.

*Identification.*—(1) Presence of large numbers of cyprids and adults in low salinity (3.4‰) waters in San Francisco Bay estuarine system (Newman, 1967; personal observation). (2) Comparison with laboratory-reared *B. im-*

*provisus* cyprids from Rhode Island. (3) Cyprid illustrations and descriptions in Buchholz (1951), Doochin (1951), and Jones and Crisp (1954); photograph in Freiberger and Cologer (1966). Naupliar stages described and figured in Buchholz (1951), Jones and Crisp (1954), and Lang (1979).

*Material examined.*—San Francisco Bay, California (October 1978).

*Diagnosis.*—Small, mean length 584 μm. Relatively opaque when preserved, especially at anterior end. No special pigmentation in preserved specimens. Carapace profile relatively high in side view; anterior end rounded; posterior end narrowly rounded; anterodorsal margin curved; posterodorsal margin curved, breaking just in front of the posterior end; ventral margin curved anterior to, and slightly curved posterior to, the compound eyes. Extreme posteroventral margin of carapace finely crenulated. Carapace profile wide in dorsal view, mean width 285 μm; with both ends rounded. Carapace sculptured with rounded pits (about 4 μm in diameter).

*Size variation.*—Mean length 584 μm, range 540 to 610 μm in San Francisco Bay, California (Table 1); mean length 587 μm in Biscayne Bay, Florida (Doochin, 1951), 523 μm on the east coast of England (Jones and Crisp, 1954), 514 μm in the Netherlands (de Wolf, 1973).

*Shape variation.*—Sometimes the anterior end is narrowly rounded in side view, and both ends are broadly rounded to truncate in dorsal view.

*Remarks.*—This cyprid is most similar to that of *C. dalli* but could also be mistaken for those of *B. glandula* or *P. polymerus*. It differs from the cyprid of *C. dalli* in having a more rounded anterior end in side view, a posterodorsal margin that breaks just in front of the posterior end, and a carapace sculptured with small pits and fine crenulations, the latter along the posteroventral margin. The sizes of *B. improvisus* cyprids do not generally overlap those of *P. polymerus* or *B. glandula,* and the sculpturing of *B. improvisus* cyprids differs from the papillae of the latter two species. In addition, unlike *P. polymerus,* the carapace peaks well behind the compound eyes in side view and is considerably wider in dorsal view. Unlike *B. glandula,* the anterior end is more evenly rounded in side view and less truncate in dorsal view. The break in the posterodorsal margin also separates the cyprid of *B. improvisus* from that of *B. glandula*. Finally, *B. improvisus* cyprids are not likely to be found along the outer coast but do occur in the upper reaches of estuaries. Therefore, they co-occur with the cyprids of *C. dalli* and *B. glandula* mainly in enclosed bays and in the mouths of estuaries.

### *Balanus glandula* Darwin, 1854
Fig. 4

*Distribution.*—Adults: upper and sometimes lower midtidal zone of exposed and protected shores; on rocks, pier pilings, and hard-shelled animals.

Cyprids: mainly high in water column; mean density 28 $m^{-3}$, 1,436 $m^{-3}$ on 26 March 1977; mainly spring, also summer and fall. Aleutian Islands south to San Quintin Bay, Baja California.

*Identification.*—(1) Coincidence of large numbers of cyprids and juveniles at collection site. (2) Adults present on pilings and floating pier adjacent to collection site. (3) Photograph of cyprid in Strathmann and Branscomb (1979). Naupliar stages have not been described or figured.

*Diagnosis.*—Medium-sized, mean length 728 $\mu$m. Translucent when fresh. Chartreuse pigmentation observable only in fresh specimens; consisting of large (5–6 times the size of the compound eye) paired, irregularly shaped areas located in posterior third of body; several small, unpaired spots posterodorsal to compound eyes; and sometimes a pair of large (2–3 times size of compound eye) paired and fused areas anterodorsal to compound eyes. Golden (or rarely brown) when preserved, with light brown cement glands ventral to compound eyes. Carapace profile high in side view, mean depth 388 $\mu$m; both ends narrowly rounded; anterodorsal margin slightly curved; posterodorsal margin evenly curved; ventral margin curved both in front of and behind compound eyes, becoming relatively straight posteriorly. Carapace profile in dorsal view fusiform, with anterior end somewhat truncate and posterior end narrowly rounded; median raphe continuous from anterior end to posterior end. When viewed from the anterior end, raphe is seen as a seam where sides of carapace meet at an acute angle along dorsal margin. Entire carapace sculptured with elliptic papillae (about 7 $\mu$m long and 2 $\mu$m wide).

*Size variation.*—Mean length 728 $\mu$m, range 640 to 780 $\mu$m at Bodega Harbor, California (Table 1); mean length 790 $\mu$m, range 670 to 860 $\mu$m on San Juan Island, Washington (Strathmann and Branscomb, 1979).

*Remarks.*—This cyprid is medium-sized, ordinarily overlapping in size only with *Balanus crenatus*. In side view it differs from the cyprid of *B. crenatus* and most other species in having a high carapace profile and a ventral margin curved well behind the compound eyes. Other distinguishing features include an anterior end somewhat truncate in dorsal view, a dorsum acutely angled rather than rounded when viewed from the anterior end, and a carapace sculptured with papillae. Also distinctive are the chartreuse-pigmented areas in fresh specimens and the golden (or rarely brown) ground color in preserved ones. Most other species are more or less white when preserved. Unlike *Balanus nubilus*? and *B. improvisus* cyprids, the carapace of *B. glandula,* in side view, has a narrowly rounded anterior end and an evenly curved posterodorsal margin. Although considerably larger than *P. polymerus,* the cyprid of *B. glandula* is similar in having the carapace sculptured with papillae. However, the papillae are elliptic rather than rounded.

*Balanus crenatus* Brugière, 1789
Fig. 5

*Distribution.*—Adults: low intertidal zone and especially subtidal areas to depths of 182 m; exposed and protected shores; on rocks, pier pilings, hard-shelled animals, and sometimes seaweeds. Cyprids: mainly low in the water column; mean density 92 $m^{-3}$, 5,909 $m^{-3}$ on 26 March 1977; summer, fall, and especially spring. Northern Japan and Alaska south to Santa Barbara, California; North Atlantic.

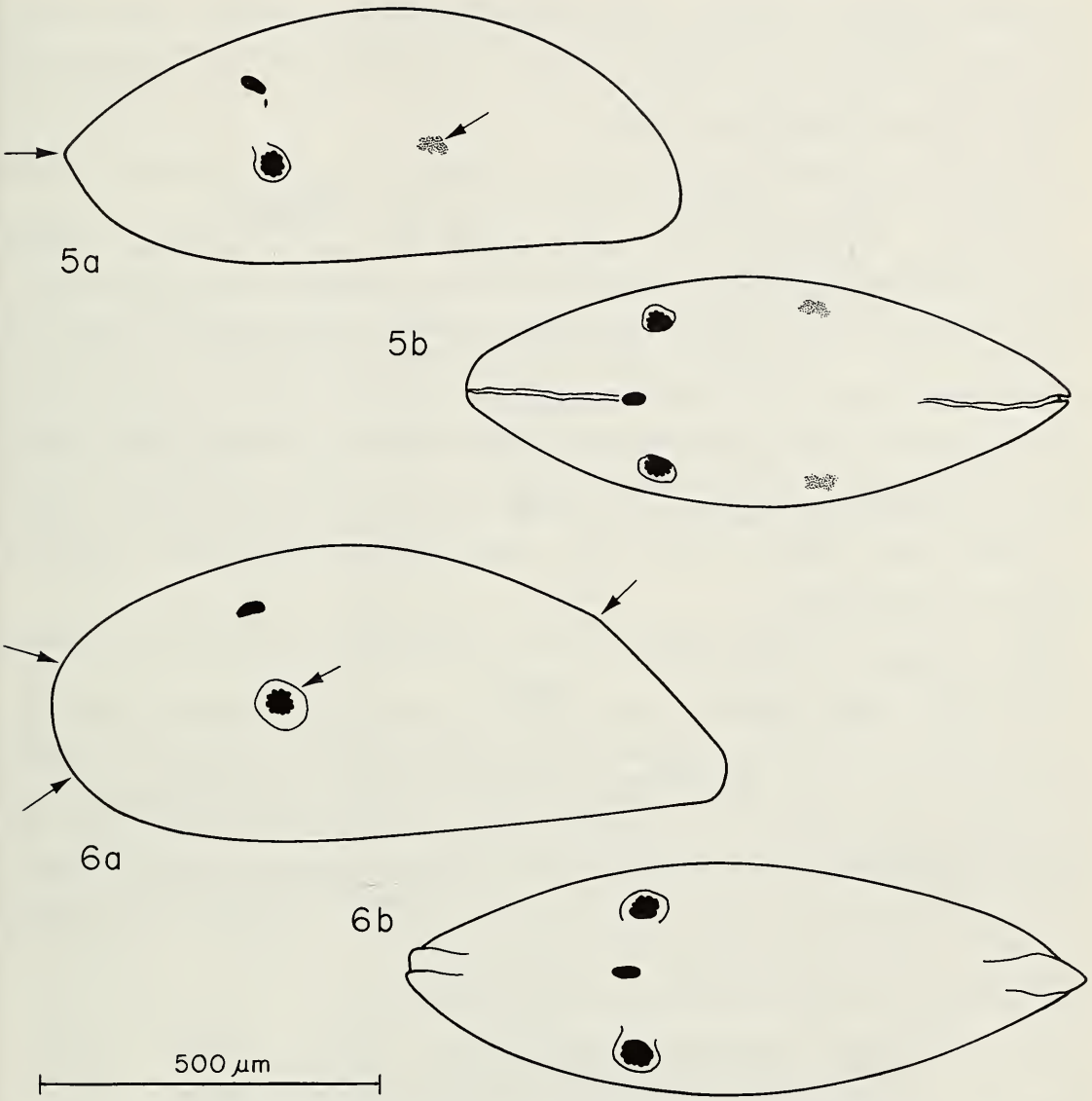
*Identification.*—(1) Juveniles reared in the laboratory from field-collected cyprids. (2) Coincidence of large numbers of cyprids and juveniles at collection site. (3) Adults present on pilings and floating pier adjacent to collection site. (4) Cyprid descriptions and illustrations in Herz (1933) and Pyefinch (1948). Naupliar stages described and figured in Herz (1933) and Pyefinch (1948, 1949).

*Material examined.*—Mostly from Bodega Harbor, California; some from Point Barrow, Alaska (August, 1976).

*Diagnosis.*—Medium-sized, mean length 852 μm. Translucent when fresh. Relatively opaque (white) when preserved, especially at anterior end. A single pair of black pigment spots, somewhat smaller than compound eyes, located just posterior to midlength, and persisting after preservation. Carapace profile low in side view, mean depth 374 μm; anterior end narrowly angular; posterior end narrowly rounded; anterodorsal margin only slightly curved; posterodorsal margin evenly curved; ventral margin curved anterior to, and relatively straight posterior to, compound eyes. Carapace profile in dorsal view fusiform, with both ends narrowly rounded. Carapace smooth, unsculptured.

*Size variation.*—Quite variable, mean length 852 μm, range 700 to 960 μm at Bodega Harbor, California (Table 1); mean length 1,001 μm, range 900 to 1,060 μm at Point Barrow, Alaska (Table 1); mean length 946 μm, range 734 to 1,102 μm in Scotland (Barnes, 1953); mean length 643 μm in the Netherlands (de Wolf, 1973).

*Remarks.*—This cyprid is most similar to that of *B. nubilus*?, a slightly larger form. It differs in having a narrowly angular anterior end in side view and an evenly curved posterodorsal margin. The cyprids of *B. glandula* and *Semibalanus cariosus* also overlap *B. crenatus* in size. However, the cyprid of *B. crenatus* has the ventral margin relatively straight behind the compound eyes and a smooth carapace, unlike *B. glandula,* and the anterior end is narrowly rounded in dorsal view, unlike both of these other species. It also differs from the cyprid of *S. cariosus* in lacking a break in the posterodorsal margin and in having a carapace profile of medium width in dorsal view. The cyprid of *B. crenatus* is distinguished from all of the above-mentioned species by having a low carapace profile in side view and a pair of black pigment spots just posterior to midlength.




Figs. 5–6. Lateral (a) and dorsal (b) views of barnacle cyprids. **5**, *Balanus crenatus;* **6**, *Balanus nubilus*?. Pigment spots are stippled. Arrows indicate some diagnostic characters used in the key.

*Balanus nubilus*? Darwin, 1854
Fig. 6

*Distribution.*—Adults: low intertidal zone and subtidal areas to depths of 90 m; exposed and protected shores; on rocks, pier pilings, and hard-shelled animals. Cyprids: mainly low in water column; mean density 6 $m^{-3}$; spring, summer, and fall, especially summer. Southern Alaska south to La Jolla, California.

*Identification.*—(1) Juveniles reared in the laboratory from field-collected cyprids. (Although identification of the juveniles was not completely certain, the presence of large numbers of this cyprid as far north as Crescent City,

California suggests that the correct identification is *B. nubilus* rather than the more southern form *Balanus aquila*.) (2) Adults present on pilings and floating pier adjacent to collecting site. Naupliar stages described and figured in Barnes and Barnes (1959).

*Materials examined.*—Mostly from Bodega Harbor, California; some from Moss Landing, California and Crescent City, California.

*Diagnosis.*—Medium-sized, mean length 932 μm. Translucent when fresh. Relatively translucent when preserved, although more opaque anteriorly and posteriorly; with light orange cement glands posteroventral to compound eyes. No special pigmentation. Carapace profile relatively low in side view; anterior end rounded; posterior end narrowly rounded; anterodorsal margin curved; posterodorsal margin curved, breaking slightly about three-fourths of the way towards posterior end; ventral margin curved anterior to, and nearly straight posterior to, compound eyes. Carapace profile in dorsal view fusiform, with both ends narrowly rounded. Carapace smooth, unsculptured.

*Size variation.*—Mean length 932 μm, range 800 to 1,000 μm at Bodega Harbor, California (Table 1).

*Remarks.*—This cyprid is most similar to that of *B. crenatus*. It differs, in side view, in having a break in the posterodorsal margin and a more rounded anterior end. This latter character also distinguishes the cyprid of *B. nubilus*? from that of *S. cariosus,* which overlap each other in size. In addition the cyprid of *B. nubilus*? has a relatively narrow width and a narrowly rounded anterior end in dorsal view, unlike *S. cariosus*. All of these characters, together with the smooth carapace of *B. nubilus*?, separate it from the cyprid of *B. glandula,* a smaller species.

Family Archaeobalanidae Newman and Ross, 1976
Subfamily Semibalaninae Newman and Ross, 1976
*Semibalanus cariosus* (Pallas, 1788) (=*Balanus cariosus*)
Fig. 7

*Distribution.*—Adults: lower midtidal and sometimes low intertidal zones of wave-exposed shores; on rocks and hard-shelled animals. Cyprids: probably low in water column; mainly spring and summer (Connell, 1970; Dayton, 1971; Strathmann and Branscomb, 1979). Japan, Bering Sea, and Alaska south to Morro Bay, California.

*Identification.*—(1) Coincidence of large numbers of cyprids and juveniles (R. R. Strathmann, pers. comm.). (2) Photograph of cyprid in Strathmann and Branscomb (1979). Naupliar stages have not been described or figured.

*Material examined.*—San Juan Island, Washington (May 1976).

*Diagnosis.*—Large, mean length 1,111 μm. Very opaque when preserved, except for translucent area along dorsum. No special pigmentation in pre-

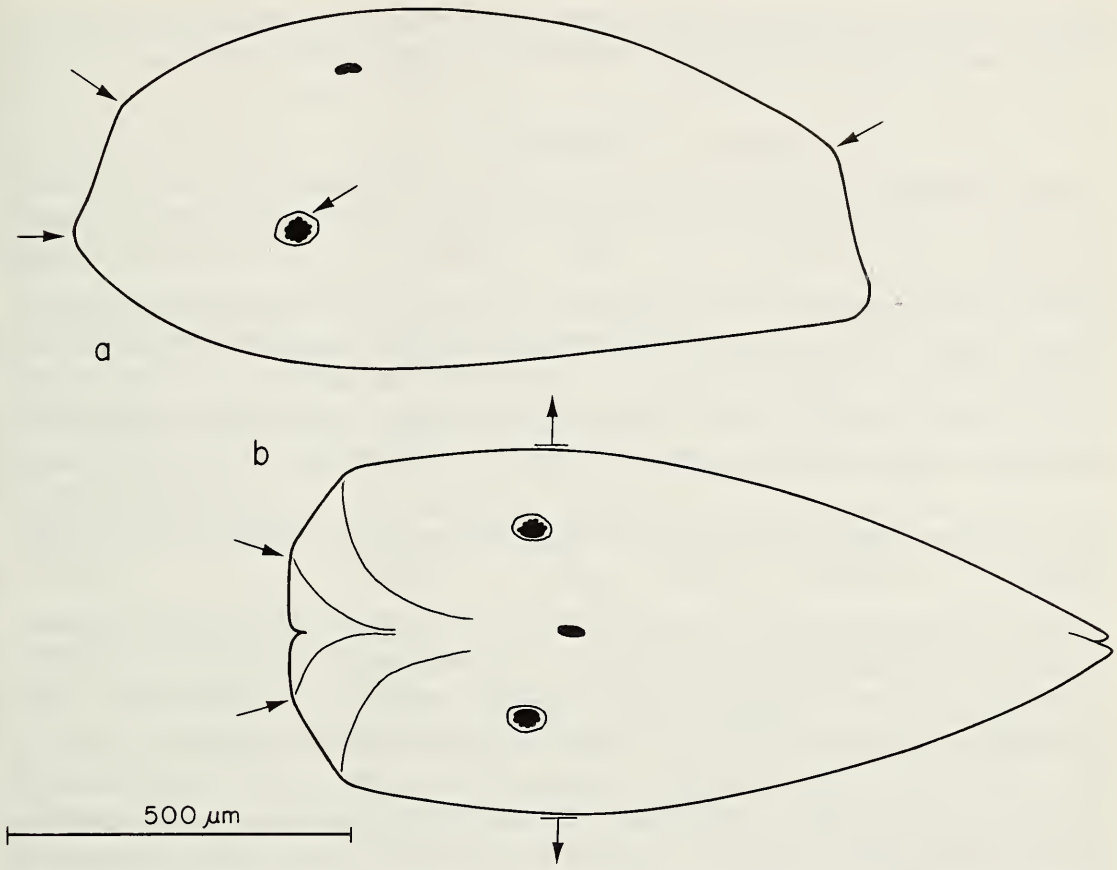



Fig. 7. Lateral (a) and dorsal (b) views of *Semibalanus cariosus*. Arrows indicate some diagnostic characters used in the key.

served specimens. Carapace profile relatively low in side view; anterior end broadly angular; posterior end narrowly rounded; anterodorsal margin curved, breaking somewhat just behind anterior end; posterodorsal margin curved, breaking prominently just in front of posterior end; ventral margin curved anterior to, and slightly curved posterior to, compound eyes. Carapace profile wide in dorsal view, mean width 493 μm; anterior end truncate; posterior end narrowly rounded. Compound eyes small and deeply inset. Carapace smooth, unsculptured.

*Size variation*.—Mean length 1,111 μm, range 960 to 1,200 μm at San Juan Island, Washington (Table 1); a larger sample (N = 80) from San Juan Island had a mean length of 1,140 μm, range 980 to 1,240 μm (Strathmann and Branscomb, 1979).

*Remarks*.—This cyprid is the largest one considered here, although its size overlaps with that of *B. nubilus*? and *B. crenatus*. It differs from the former species in having a broadly angular anterior end in side view and in having a wide carapace profile, a truncate anterior end, and relatively small, deeply inset compound eyes, all visible in dorsal view. These characters,

together with the breaks in the anterodorsal and posterodorsal margins of *S. cariosus,* serve to distinguish it from the cyprid of *B. crenatus.*

## Discussion

Over 50 species of thoracican cyprids have been previously illustrated or described, mostly from the North Atlantic, India, and Australasia (cf. Nilsson-Cantell, 1921, 1978; Lang, 1979). The present paper describes seven species of cyprids from the Oregonian Province of the temperate Northeast Pacific region. They include most of the intertidal barnacles characteristic of this province, along with some of the more subtidal forms. The ranges of most of these species extend into the adjoining Aleutian and Californian Provinces, where still other species occur. Nevertheless, the descriptions given here will account for most of the intertidal species encountered in the Aleutian and Californian Provinces; they will be less useful for the subtidal species.

The taxonomic features studied here were size, shape, special pigmentation, and sculpturing. Size is usually expressed in the descriptive literature as carapace length; carapace depth appears occasionally, width rarely. Cyprids range in length from less than 100 $\mu$m (Bocquet-Védrine, 1961) to more than 2,200 $\mu$m (Standing, personal observation). The very smallest cyprids, in general, are rhizocephalans, while lepadids and some scalpellids tend to be very large (Nilsson-Cantell, 1921; Zevina, 1971). Other scalpellids are considerably smaller. For example, *Calantica spinosa* and *Pollicipes polymerus* have lengths of 850 $\mu$m and 494 $\mu$m, respectively (Batham, 1946b; the present study). The trends in the Balanomorpha are as follows: chthamaloidean cyprids are small (less than 625 $\mu$m), but not as small as rhizocephalans; coronuloideans are mostly small to medium sized; and balanoideans range from small to large, although *Chirona hameri* is very large, averaging 1,454 $\mu$m (Crisp, 1962). The smallest and largest balanoidean cyprids observed in the present study were *Balanus improvisus* and *Semibalanus cariosus,* respectively (Table 1).

Cyprid size is quite variable, even within a single species. In the laboratory, size varies inversely with rearing temperature (Lang, 1979), and in the field, size often varies directly with latitude (Pyefinch, 1948; Crisp, 1962). This size-latitude phenomenon, probably involving both temperature and food supply, also applies to barnacle nauplii and embryos (Barnes and Barnes, 1965), as well as many other marine animals. The present study provides additional evidence of the size-latitude phenomenon. *Balanus crenatus* cyprids from Point Barrow, Alaska, were larger than those from Bodega Harbor, California (Table 1), and *B. glandula* cyprids from San Juan Island, Washington (Strathmann and Branscomb, 1979) were larger than those from Bodega Harbor.

Some species of cyprids in the present study overlapped considerably in size (Table 1). For this reason, size is best considered a taxonomic feature of secondary importance. However, it is useful for initially distinguishing between groups of species and for helping to recognize species after initial identification. Carapace width was a good character for separating *Pollicipes polymerus* and *Semibalanus cariosus* cyprids from other species of similar length.

Carapace shape characters, unlike size, proved to be particularly important for discriminating between species. Therefore, shape characters have been described in detail and illustrated carefully, operations not always accomplished in previous studies. Still, the existing literature does suggest the variation to be expected in shape characters, and some general trends in cyprid shapes.

Side views of shape characters are especially revealing. The anterior ends of cyprids vary from pointed or angular through rounded to truncate. Anterodorsal margins are usually inflated to various extents but can be depressed. *Pollicipes polymerus* has a broadly rounded anterior end and a broadly curved anterodorsal margin, resembling *Calantica* (formerly *Pollicipes*) *spinosa* but not *Capitulum* (formerly *Pollicipes*) *mitella* (Yasugi, 1937; Batham, 1946b). Also similar in these respects are some other scalpellids and most lepadids (Darwin, 1851; Aurivillius, 1894; Nilsson-Cantell, 1921; Broch, 1931; Zevina, 1971). *Chthamalus dalli* has an angular anterior end similar to that of some other chthamalids (Barker, 1976; Karande and Thomas, 1976; Lang, 1979), but it is unclear whether or not this character is representative of the group. The break in the anterodorsal margin of *Semibalanus cariosus* cyprids is a character different from any other illustrated in the literature.

Posterior ends of cyprids range from sharply pointed through narrowly rounded to broadly rounded; posterodorsal margins are usually inflated to varying degrees but can be depressed. Some species of cyprids have angular (i.e., "broken") posterodorsal margins: *Pollicipes polymerus, Balanus improvisus, B. nubilus*?, and *Semibalanus cariosus* in the present study. The literature suggests that this character is more common in lepadomorphs (Aurivillius, 1894; Broch, 1931; Anderson, 1965; Standing, personal observations) than in balanomorphs (Buchholz, 1951; Moyse, 1961), but it is also likely that the character has frequently been overlooked in previous studies. Another interesting character on the posterior end is the finely crenulated margin of *Balanus improvisus,* a character similar to that present in the acrothoracican *Trypetesa nassaroides* (Turquier, 1967). This character is reported here for the first time in *B. improvisus* from San Francisco Bay (and from Rhode Island), even though the cyprid has been illustrated many times before. It is not yet clear whether this character is representative of

the species and previously overlooked, or present in only some populations. The existing illustrations of this species suggest that other characters may be quite variable as well.

Ventral margins also differ between species. They may be straight through curved to recurved. Most species have convexly curved ventral margins. However, *Pollicipes polymerus* cyprids and those of some other lepadomorphs have relatively straight ventral margins (Darwin, 1851; Aurivillius, 1894; Broch, 1931; Batham, 1946b; Zevina, 1971).

Dorsal views of cyprids show fewer shape characters than side views. Nevertheless, some of these characters have taxonomic value. Particularly interesting are anterior ends, which can vary from angular through rounded to truncate. Most species have rounded anterior ends, but those of *Balanus glandula* and *Semibalanus cariosus* are nearly truncate. The curvature of the sides and the shape of the posterior end also vary in cyprids, but these characters appear to have less taxonomic value than some of the other characters, at least in balanomorphs.

Carapace sculpturing characters are infrequently referred to in the descriptive literature. The present study suggests that they may be more widespread than is generally believed, but often overlooked. At present a number of lepadomorphs are known to have parallel carinae along the length of the carapace (Darwin, 1851; Broch, 1931; Batham, 1946a, b; Zevina, 1971; Standing, unpublished observations), and "brickwork" sculpturing has been described for *Ibla cumingi* (Karande, 1974). In addition, *Semibalanus balanoides* has tiny pits (Walker and Lee, 1976), which appear to be similar to those observed for the first time here on *Balanus improvisus* from San Francisco Bay (but not on specimens from Rhode Island). However, the papillae described here for *Pollicipes polymerus* and *Balanus glandula* cyprids are different from any sculpturing previously described, including the papillae that occur on the ascothoracican *Ulophysema öresundense* (Brattström, 1948) and the "peg-plates" present on some acrothoracicans (Tomlinson, 1969). Some acrothoracican and rhizocephalan cyprids also have the carapace ornamented with large spines, but these are very different from the small spine-like processes seen on *Pollicipes polymerus*. Clearly, much additional work is needed to fully assess the importance of carapace sculpturing and ornamentation to cyprid taxonomy. SEM studies, for example, might reveal ultramicroscopic sculpturing in species that appear smooth under the light microscope.

Special pigmentation characters, like sculpturing characters, are not often mentioned in the literature, probably because most species lack them. The positions of pigment spots or areas seem to vary widely in different species, but in general, cyprids with special pigmentation can be conveniently divided into two color classes: those having bright yellow or orange areas of pigmentation (Batham, 1946b; Walley, 1969; Lang, 1976) and others having

dark purple or black pigmentation (Pillai, 1958; Barker, 1976). In the present study, chartreuse areas were observed in fresh *Balanus glandula* cyprids, and black spots were present on *B. crenatus*. The pigmentation in *B. glandula* cyprids appears to be similar to the "yellow cells" found in *Semibalanus balanoides* (Walley, 1969); the spots in *B. crenatus* cyprids may be most similar to the "black patches" described for *Balanus amphitrite amphitrite* (Pillai, 1958), and also present on *B. improvisus* from Rhode Island (Standing, personal observation). The special pigmentation observed in the cyprids of *B. glandula* and *B. crenatus* has not been previously reported, although both species have been briefly described before.

Distributional information can also be useful in larval identification, but it must be interpreted carefully. Cyprids are likely to be found outside the geographical ranges of adults only occasionally, and inshore species are not often collected far out to sea, at least in the Oregonian Province. A few species may be found in special situations where other species are not to be expected. *Balanus improvisus* cyprids, for example, occur in very low salinities that probably cannot be tolerated by other species. Although they have been collected in bays and estuaries on this coast, they were not taken at Bodega Harbor and are probably not ordinarily present along the outer coast. Another cyprid not collected at Bodega Harbor was *Semibalanus cariosus,* although adults are present in the area. The adults of this species become uncommon south of San Francisco, and recruitment may be infrequent in central California. Vertical distributions in the water column and seasonal abundances of cyprids also differ, but identifications should not be based on this information because of considerable overlap between species. The ecological data collected in the present study will be presented in greater detail elsewhere.

In conclusion, the present work has shown considerable differences between some species of cyprids present in the Oregonian Province. Application of microdissection and electron microscope techniques will undoubtedly reveal further variation. Even now, the differences separating the cyprids of *Balanus improvisus, B. glandula,* and *B. crenatus* may be greater than those known to separate the juveniles or adults of these species. Further study of cyprids, like nauplii (Lang, 1979), should enable us to view the life histories and phylogenies of cirripedes in new and revealing ways.

## Key to Cyprids of the Oregonian Province

1. Small, length less than 625 $\mu$m ..... 2
– Medium to large, length greater than 625 $\mu$m ..... 5
2. Anterior end narrowly rounded to angular in side view; posterodorsal margin evenly curved (Figs. 2a, 4a) ..... 3

– Anterior end broadly rounded to rounded in side view; posterodorsal margin with break in curve (Figs. 1a, 3a) ..... 4

3. Distinct golden (rarely brown) ground color when preserved, chartreuse pigmented areas when fresh; carapace surface dull under low magnification, sculptured with papillae under high magnification .. ..... *Balanus glandula*[2] (Fig. 4)

– Relatively translucent when preserved, no special pigmentation when fresh; carapace surface shiny under low magnification, smooth under high magnification ..... *Chthamalus dalli* (Fig. 2)

4. Carapace depth greatest about one-third of the way back from anterior end; carapace breadth narrow in dorsal view, about one-third length; mainly outer coast ..... *Pollicipes polymerus* (Fig. 1)

– Carapace depth greatest about halfway back from anterior end; carapace breadth wide in dorsal view, about one-half length; bays and estuaries ..... *Balanus improvisus* (Fig. 3)

5. Anterior end narrowly angular to narrowly rounded in side view; posterodorsal margin evenly curved (Figs. 4a, 5a) ..... 6

– Anterior end broadly angular to rounded in side view; posterodorsal margin with break in curve (Figs. 6a, 7a) ..... 7

6. One pair of black pigment spots just posterior to midlength when fresh; white ground color when preserved, with pigment spots persisting; carapace surface shiny under low magnification, smooth under high magnification ..... *Balanus crenatus* (Fig. 5)

– Several chartreuse pigmented areas when fresh; golden (rarely brown) ground color when preserved, with no special pigmentation persisting; carapace surface dull under low magnification, sculptured with papillae under high magnification *Balanus glandula* (Fig. 4)

7. Anterior end truncate, posterior end narrowly rounded in dorsal view; carapace breadth wide in dorsal view, about one-half length; compound eyes small, eye capsules less than 68 μm ..... ..... *Semibalanus cariosus* (Fig. 7)

– Anterior and posterior ends both narrowly rounded in dorsal view; carapace breadth relatively narrow in dorsal view, about one-third length; compound eyes large, eye capsules more than 68 μm ..... ..... *Balanus nubilus*? (Fig. 6)

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[2] Only rarely less than 625 μm in length.

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